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ORIGINAL ARTICLE

Iranella inopinata Gollestaneh 1965, a puzzling dasycladalean alga from the Lower Cretaceous shallow carbonate shelf deposits of the Zagros fold-thrust belt, SW Iran

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Abstract *Iranella inopinata* gen. and sp. nov. was first described in the unpublished thesis of Gollestaneh (1965), as an incertae sedis from the Lower Cretaceous carbonate rocks of the Zagros fold-thrust belt. More recently, the taxon was formally, although provisionally described by Hosseini and Conrad (Geol Croat 61:215–237, 2008), as a dasycladalean alga named *Salpingoporella*? *inopinata*. Here, based on the interpretation of quite-abundant although scattered fragments, it is assigned to *Iranella*, a large-sized, stalked, and capitulum-shaped new genus of Dasycladales. The lower, stalked part of the thallus is cylindrical, strongly calcified, with first-order laterals only, while the large capitulum is only partly calcified, showing one or two orders of laterals. Traces of cysts (reproductive organs) are present in the basal stalk, either in the stipe or the laterals. *Iranella inopinata* looks to be endemic to the southwestern part of the Tethyan realm, in the Zagros area and also south of the Persian Gulf. In the Zagros Mts., it extends from the Berriasian to the Aptian, with an Acme Zone in the Valanginian. Sequential interpretation proves the presence of this species in the late transgressive and early highstand stages of system tracts, and reveals a low-energy, restricted, lagoonal or back-reef depositional environment, in an inner-platform setting.

Keywords Iranella · Dasycladales · Systematics · Lower Cretaceous · Zagros · Iran

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Introduction

The Zagros fold-thrust belt (ZFTB) corresponds to the southwestern part of the Tethyan realm and northeastern part of the Arabian Platform. In this area (Fig. 1), Lower Cretaceous shallow carbonate shelf deposits typically contain algal-rich wackestones, packstones, and peloidal grainstones of shallow shoal origin. These deposits were investigated from 14 outcrops in an effort to elaborate a high-resolution biostratigraphic scheme, a sequential interpretation, and configuration of the platform. During this study, we found new data on *Iranella inopinata*, a dasycladalean alga originally and provisionally described by Gollestaneh (1965) as an incertae sedis. This study focuses on the taxonomy, habitat, and systematic affinities of this taxon. New for the record, a number of specimens belonging to *I. inopinata* were measured and analyzed in axial, transversal, and tangential sections, enabling us to better understand the morphology of this form.

Geological framework

The Zagros FTB results from the collision of the Arabian Platform with the continental blocks of the Central Iran

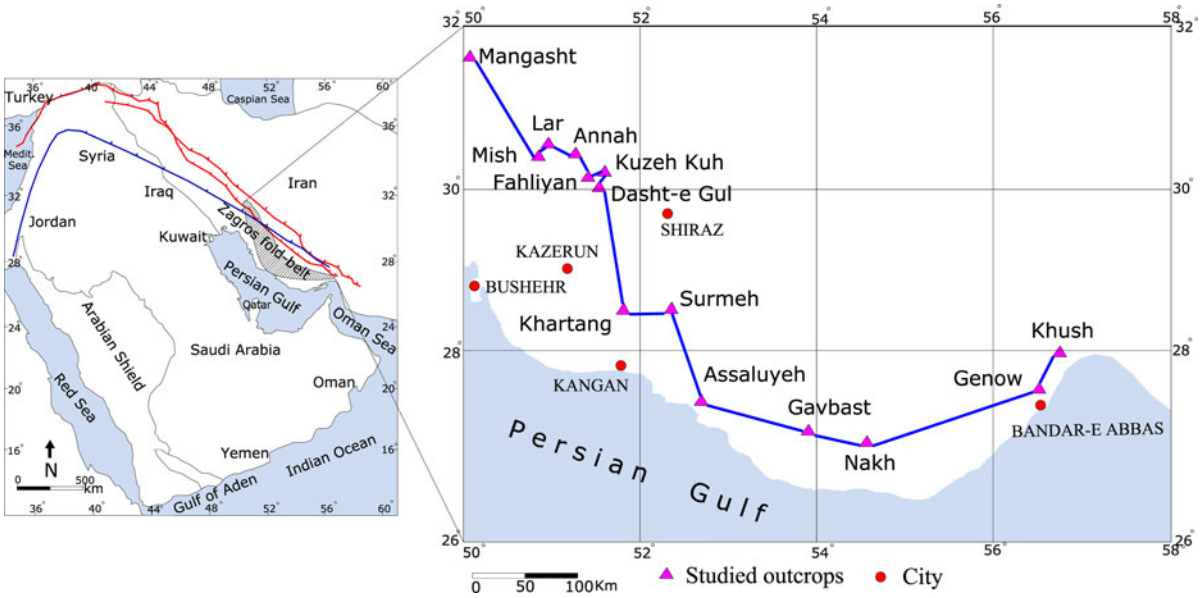

Fig. 1 The Arabian Platform and simplified location map of the studied exposures in the Zagros fold-thrust belt. Modified from Haq and Al-Qahtani (2005)

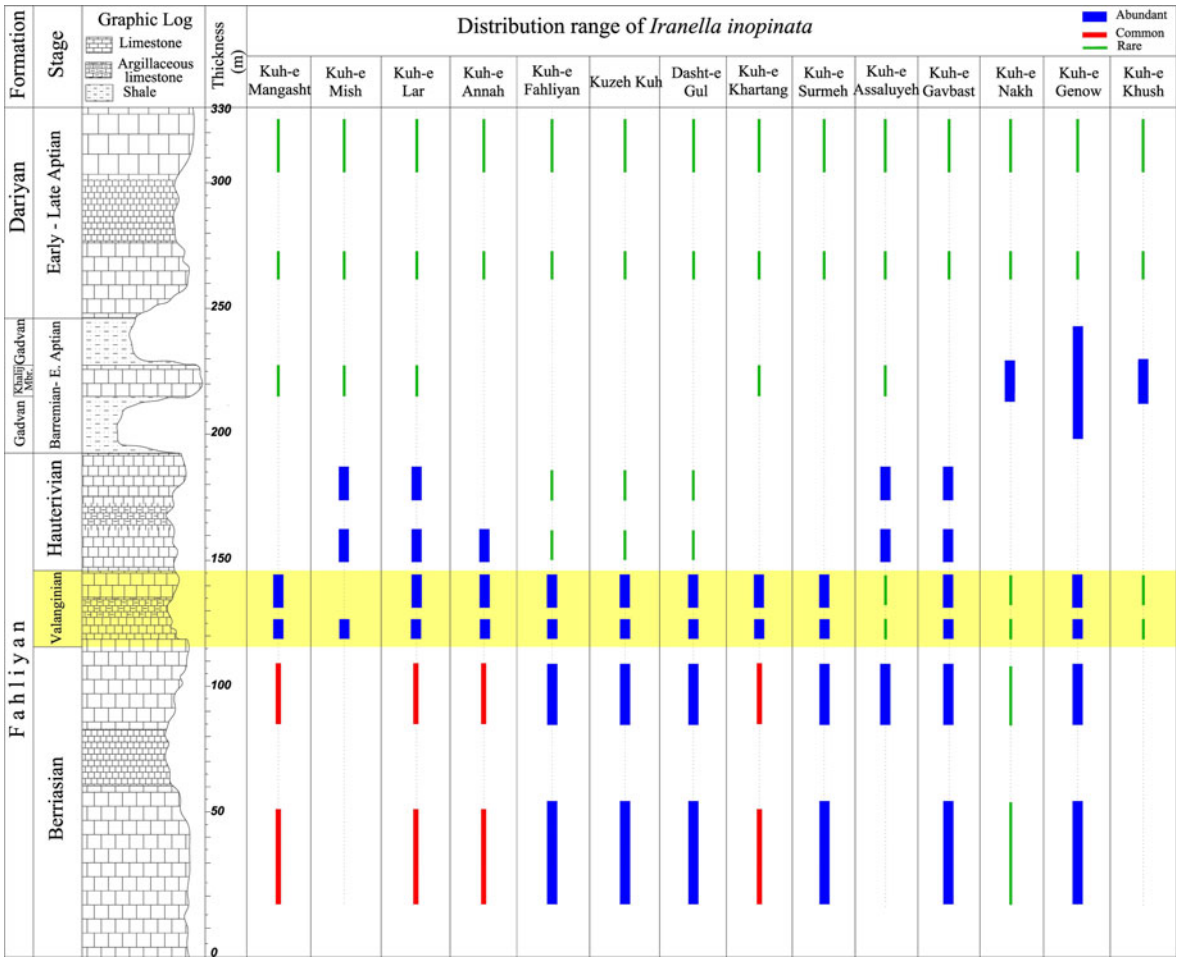

Fig. 2 Overview of the Lower Cretaceous lithostratigraphy in the study area (Zagros fold-thrust belt) and semi-quantitative distribution of *Iranella inopinata*. Thicknesses and pattern of formations are schematic

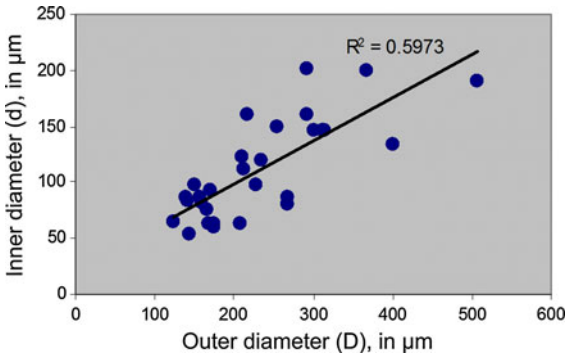

Fig. 3 Straight regression line of a d/D scatter diagram relating to the basal stalk of *Iranella inopinata*

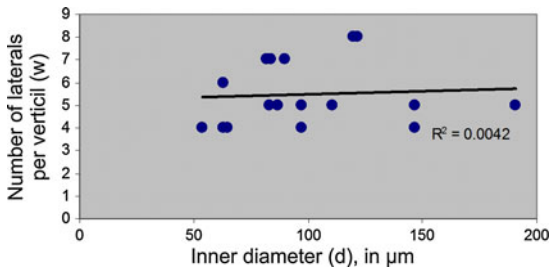

Fig. 4 Scatter diagram for w/d relating to the basal stalk of *Iranella inopinata*

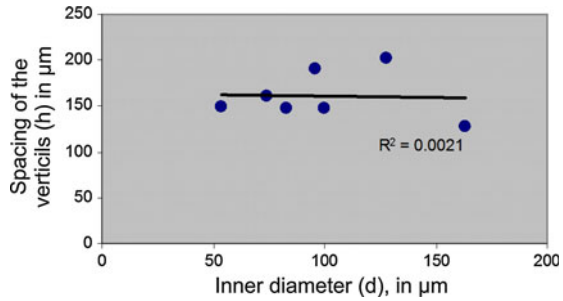

Fig. 5 Scatter diagram for h/d relating to the basal stalk of *Iranella inopinata*

(Stöcklin 1968). The folding mainly occurred during the Mio-Pliocene by the end of deposition of the Agha-Jari Formation, about 3–7 Ma ago (Falcon 1961; Berberian and King 1981), while the final collision of Arabia-Eurasia culminated. The studied lithostratigraphic units belong to the Fahliyan, Gadvan, and Dariyan formations in the Zagros FTB, on the northeastern side of the Arabian Platform. They are well exposed, forming extensive outcrops of the mentioned sedimentary successions in the studied area (Figs. 1, 2). The lowest unit of the Lower Cretaceous succession is the Fahliyan Formation, which essentially consists of shallow-water, internal platform limestones in the Berriasian–Hauterivian interval. Elsewhere in the Arabian Platform, age-equivalent units are the Yammama, Minaghish, Habshan, Lekhwair, and Ratawi formations (Shebl and Alshahran 1994, 2000; Sharland et al. 2001). The Fahliyan Formation is divided into two parts: the Lower Fahliyan includes thick to massive limestone beds with textures mostly varying from wackestone to grainstone, and bindstone in some parts, while the upper part of the formation is comprised of thin to medium argillaceous limestone beds, and with some intercalations of shale. The Barremian—Early Aptian Gadvan Formation compares to the Buwaib, Lekhwair, and Kharaib formations in the Arabian Platform (Sharland et al. 2001, 2004). This formation mostly comprises shale and thin argillaceous limestone beds. A clean carbonate unit called Khalij Member occurs in the middle part of the Gadvan Formation, forming a marker bed that can be traced over hundreds of kilometers across the Zagros FTB. The last unit, the Dariyan Formation, shows as an open-platform depositional environment with orbitolinid-rich limestone deposits. It compares to the Shuaiba Formation in the Arabian Platform (Sharland et al. 2001, 2004).

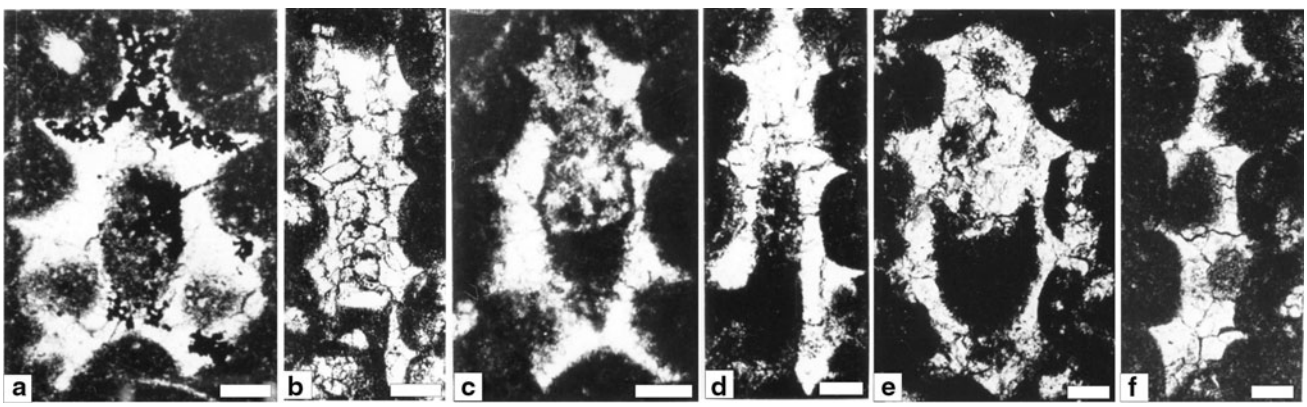

Fig. 6 Some sections labeled *Iranella inopinata* gen. and sp. nov. by Gollestaneh (1965, pls. 68–69), Berriasian-Aptian, Zagros Basin (Tang-e Godar Moshk, Kuh-e Namak, Kuh-e Qaleh Shur, and Kuh-e Gavbast). Here, these sections are interpreted as cutting the basal stalk of the alga. **a**, **c**, **e** Oblique–transversal sections, **b** sub-axial, longitudinal section, **d** oblique-tangential section of the stalk and basal part of the capitulum, **f** tangential section. *Scale bars* 50 µm

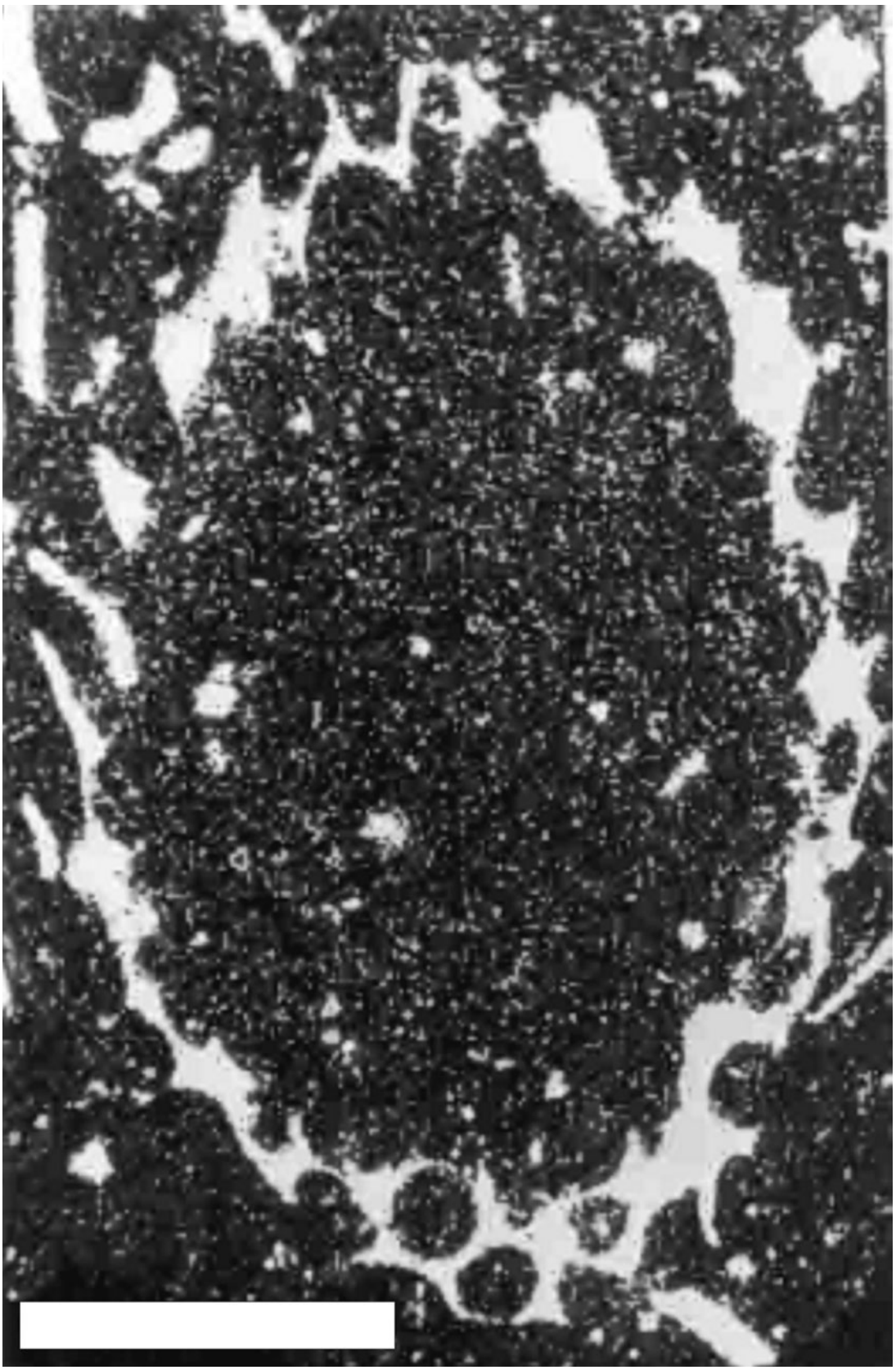

Fig. 7 *Iranella* ? aff. *inopinata*. Oblique section of a large alga assigned to *Macroporella gigantea* by Gollestaneh (1965, pl. 54, fig. 1), Kuh-e Kalagh. *Scale bar* 500 μm

Materials and methods

Fourteen surface sections (Fig. 2) were sampled and studied for their algal facies and foraminiferal content. More than 100 fragments of *I. inopinata* were studied and measured in various sections in an effort to delineate a dimensional continuum in the morphological components of the alga. Complete specimens showing all taxonomic facets are yet missing in our collection, however. Four enumerative and dimensional parameters relating to the basal stalk of the alga were measured in axial, transversal, and tangential sections, enabling to draw several diagrams showing significant linear relationships between different variables, with an acceptable standard deviation (Figs. 3, 4, 5). Combined with important taxonomic characters, such as the presence of a basal stalk followed by a costulated capitulum, this data enabled us to entirely revise the original description (as an incertae sedis) by Gollestaneh (1965), the subsequent, provisional protologue of Hosseini and Conrad (2008), and formally describe a new genus of dasycladalean alga.

The taxon was formally, although provisionally, described by Hosseini and Conrad (2008) as a dasycladalean alga named *Salpingoporella*? *inopinata*. Here, the holotype is illustrated in Fig. 11. Ultimately, new investigations carried out on a number of new thin-sections have shown the presence of a two-fold taxonomic arrangement, the basal, heavily calcified stalk of the alga being topped by a large, costulated but incompletely calcified capitulum (head) comprising, in some cases second order laterals. To date, interpretation of this new data is still not entirely satisfactory. In particular, a complete specimen of the alga is still missing. It encourages us, however, to formalize the genus *Iranella* Gollestaneh and describe, at least for the time being, the main characters of this so-far-monospecific taxon assigned to the family Triploporellaceae.

Systematic paleontology

Division Chlorophyta
Order Dasycladales Pascher, 1931
Family Triploporellaceae Pia, 1920, sensu Barattolo et al., 2008
Iranella ex Gollestaneh, 1965 n. gen.

Type species *Iranella inopinata* Gollestaneh, 1965 ex Hosseini and Conrad, 2011, n. comb.

Diagnosis: Thallus clavate or similar, euspondyl with a conspicuous basal stalk holding a large, costulated capitulum. Laterals phloiophorous, uncalcified at tip. One order of laterals in the stalk, one or two in the capitulum. Reproduction: endosporous or cladosporous. Calcification standard (originally aragonitic), conspicuous in the stalk, incomplete, peripheral only in the large capitulum.

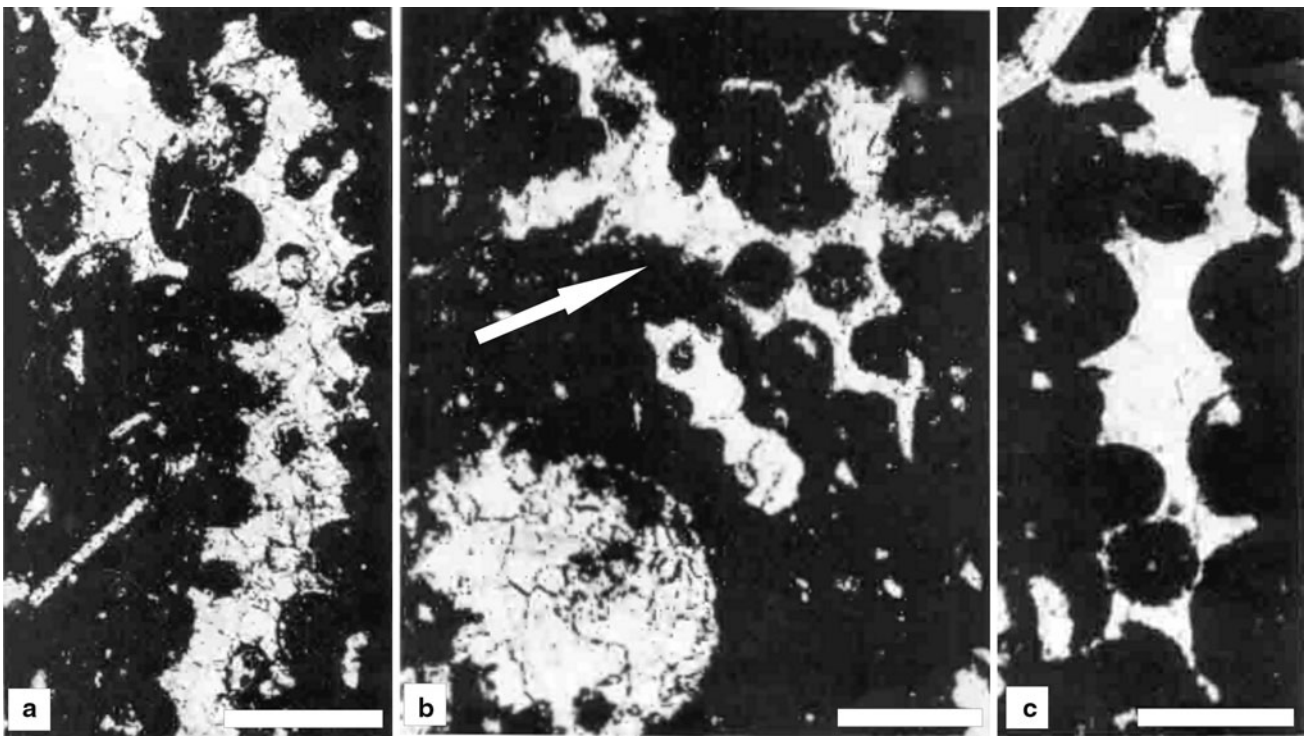

Fig. 8 Transversal - tangential sections through the capitulum of *Iranella inopinata* which had been assigned to *Macroporella gigantea* by Gollestaneh (1965, pl. 54, figs. 2-4), Kuh-e Gavbast. *Scale bars* 300 μm

Comparisons. The genus is so far monospecific. Comparisons are given below under *I. inopinata*.

Iranella inopinata Gollestaneh, 1965 ex Hosseini and Conrad, 2008, n. comb., Figs. 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19.

1965 *Iranella inopinata*, gen. and sp. nov.—Gollestaneh: 250, pls. 68, 69; pro parte pl. 54 [under *Macroporella gigantea*]; ? pl. 72, figs. 1, 2 [under *Cylindroporella sugdeni*].

2008 *Salpingoporella*? *inopinata*—Hosseini and Conrad: 216, pl. 1, figs. J–N, ?T; pl. 2, figs. N–P; pl. 4, figs. D, I, L–P.

Holotype: Specimen JHT1317 (Fig. 11) of Hosseini and Conrad (2008, pl. 1, fig. L), deposited in the Department of Geological studies and researches of the Exploration Directorate of the National Iranian Oil Company (NIOC), A. Gollestaneh's collection.

Diagnosis: As for the genus.

Dimensions of the basal stalk: Length = up to 5,000 μm; inner diameter (*d*) = 63–200 μm; outer diameter

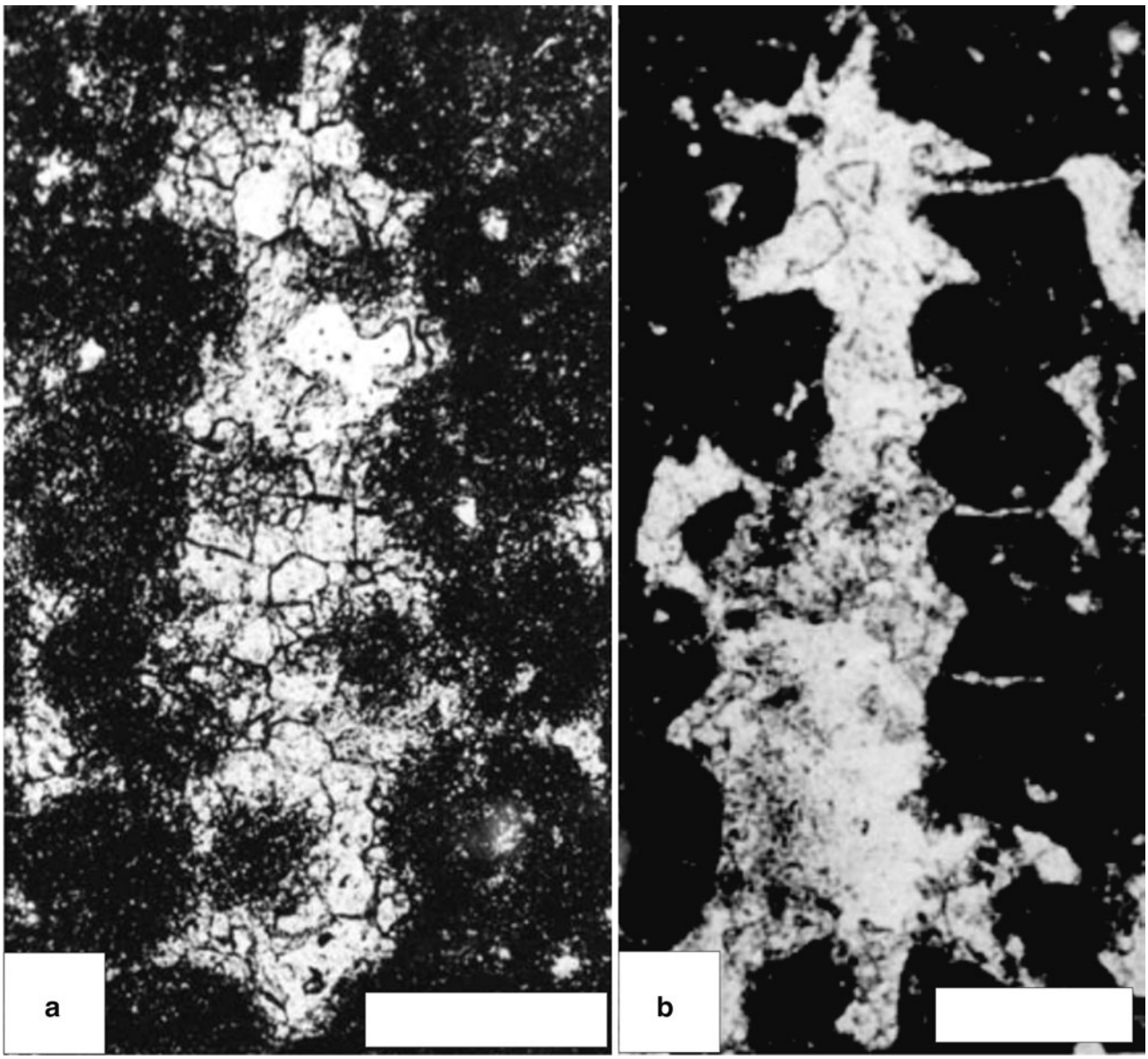

Fig. 9 Questionable sections, possibly tangential to the capitulum of *Iranella inopinata* but assigned to *Cylindroporella sudgeni* by Gollestaneh (1965, pl. 72, figs. 1–2), Kuh-e Gavbast (**a**) and Surmeh (**b**). *Scale bars* **a** 200 μm, **b** 300 μm

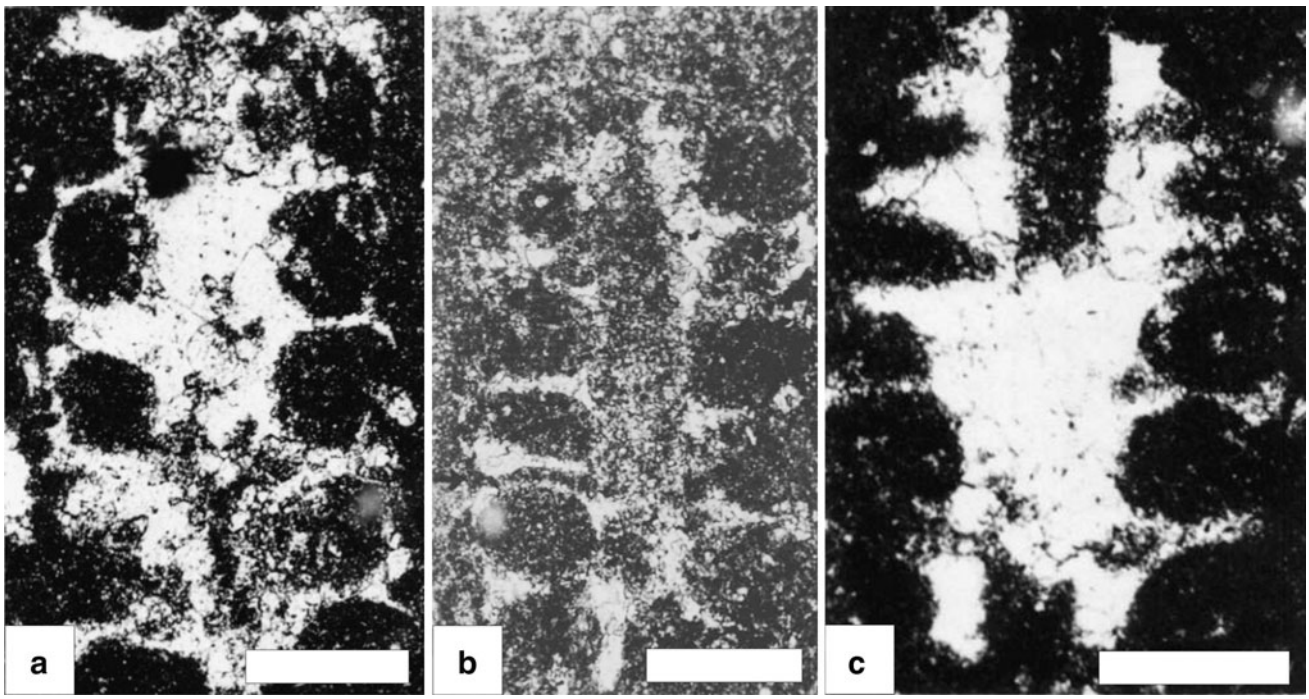

Fig. 10 Sections assigned to *Cylindroporella arabica* by Gollestaneh (1965, pl.123, figs. 1-3), Kuh-e Surmeh and Sirmand, not to be confused with *Iranella inopinata*. *Scale bars* **a** 10 0 μm; **b**, **c** 150 μm

(D) = 125–508 μm; d/D ratio = 0.4–0.5; spacing of the verticils (h) = 54–222 μm; number of laterals per verticil (w) = 4–8; diameter of the cysts = 5–10 μm.

These values are global, aggregating all studied samples. In fact, while rather uniform in a given sample, they vary significantly from one sample to another, most likely depending on the hydrodynamic sorting in the depositional environment, and/or the algal habitat. As an example, specimens from the Barremian—Early Aptian Gadvan and Aptian Dariyan formations are commonly (but not always) undersized, looking stunted with respect to older specimens from the Fahliyan Formation.

The scatter diagram for d/D ratio (Fig. 3) shows a significant, logical degree of correlation coefficient between the two variables through the studied samples, suggesting that although the values greatly vary in different samples, they correspond to the same species. The trend of the w/d scatter diagram suggests that there is only a small increase of the number of laterals per verticil against an increasing width of the inner diameter (Fig. 4). Another diagram, h/d (Fig. 5), reveals that the spacing of the verticils remains mostly consistent upon increase of the inner diameter.

Description and remarks: The original, invalid description is as follows: "Small hollow cylindrical (tapering toward the growing end) calcareous bodies, nodal, with alternating concave facets, many-sided in cross section". Some of the specimens illustrated by Gollestaneh (1965) are shown in Fig. 6. Worth mentioning, certain sections assigned by this author to *Cylindroporella sudgeni* (pl. 72, figs. 1–2, Kuh-e Gavbast and Surmeh) and *Cylindroporella arabica* (pl. 123, figs.1–3, Kuh-e Surmeh and Sirmand), may be confused with *Iranella inopinata*. Here, they are reproduced in Figs. 9 and 10.

Sections in the stalk are illustrated in Figs. 6, 11, 12, 13, 14, with tentative, schematic reconstructions. The stipe is cylindrical, or slightly constricted at level of the verticils. In the stalk, dimensions and enumerative values such as the number (w) of laterals per verticil and the inner to outer ratio (d/D) vary considerable, possibly reflecting environmental bias rather than corresponding to growth stages of the alga. Imprints of cysts are usually missing, but in several cases are definitely visible either in the stipe (endospory, Fig. 13) or in the laterals (cladospory, Fig. 14). In the holotype for example (Fig. 11), the laterals arise from a narrow proximal pore. Thereafter they open out rapidly, freely (circular or oval in section), alternate among contiguous verticils, and are distally uncalcified, presumably forming a cortex similar to *Salpingoporella*. Rare sections showing the transition (junction) between the stalk and the capitulum are illustrated in Figs. 6d, 15, again with a tentative reconstruction.

Axial and transversal reconstructions of the capitulum (Figs. 15, 16, 17, 18) are tentative, for complete specimens showing the upper part of the capitulum are yet missing. Typically, only a single (?primary) order of laterals is visible, distally forming a staggered pattern of vertical

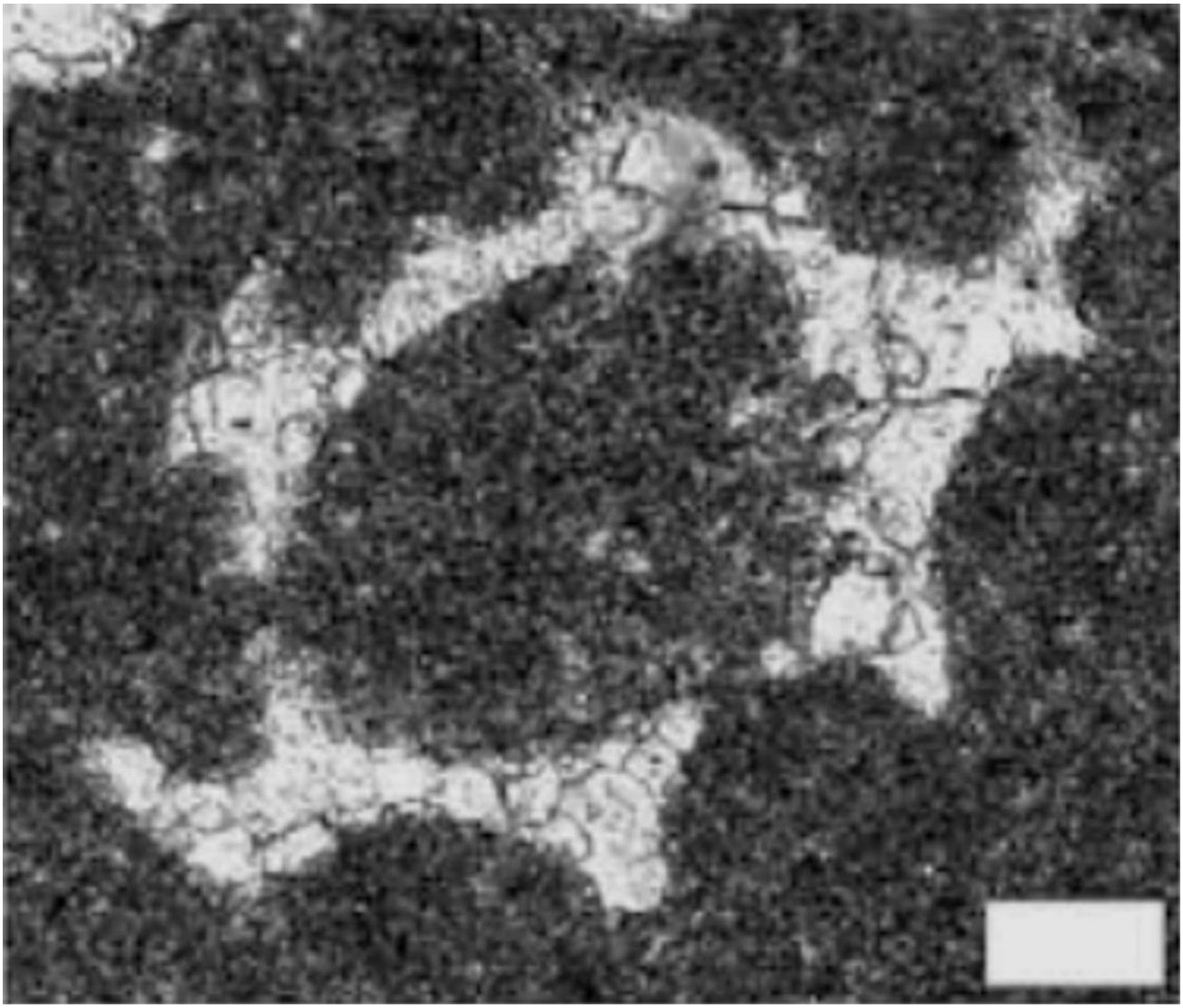

Fig. 11 *Iranella inopinata*, the holotype. Oblique section of the stalk, with imprints of cysts in the laterals (locations shown in Fig. 14). Late Berriasian, Kuh-e Surmeh, sample No: JHT 1317 of Hosseini and Conrad 2008, pl. 1, fig. L). *Scale bar* 50 μm

(axial) and horizontal (transversal) rows. The laterals are usually more or less perpendicular to the surface of the capitulum. In one case, however, they are markedly bent (Fig. 7), thus possibly corresponding to another taxon. Distally, the laterals pertaining to contiguous rows are joined together, staggered, either more or less free, circular, or oval in section (e.g., Figs. 6b, 15; section MAK5296) or, seldom, mutually compressed, polygonal (Fig. 16). In some cases (Fig. 16), tiny holes (pores) are found in the calcified area separating two laterals, suggesting the presence of sterile hairs, a feature found in other dasycladalean alga, and considered of little or low significance for the systematic. Below this (visible) periphery of the capitulum, the space left between the vertical (axial) rows is heavily calcified, forming stiff costules (Figs. 16, 17), a rare feature possibly contributing to the bearing of the alga.

Less commonly, two orders of laterals are visible at the periphery of the capitulum. As illustrated and reconstructed in Figs. 18, 19, longitudinal, calcified costules also occur in this case, on top of rather large, ?primary laterals. Higher-order, ?secondary laterals are four in number and phloiophorous. They are not clustered at the base, but arise laterally from the rounded tip of the primaries, enclosing the calcified costules and forming a distal cortex. Again, narrow holes, circular in section are present, suggesting the presence of sterile hairs. Distal sections, tangential to these rather questionable secondaries are illustrated in Fig. 18, section MAK 5025.

Systematics, comparisons: In *Iranella inopinata*, reproductive organs (cysts) are either missing (not visible), or they are present in the basal stalk, whichever within the stipe (endospory), or the laterals (cladospory). This, highly

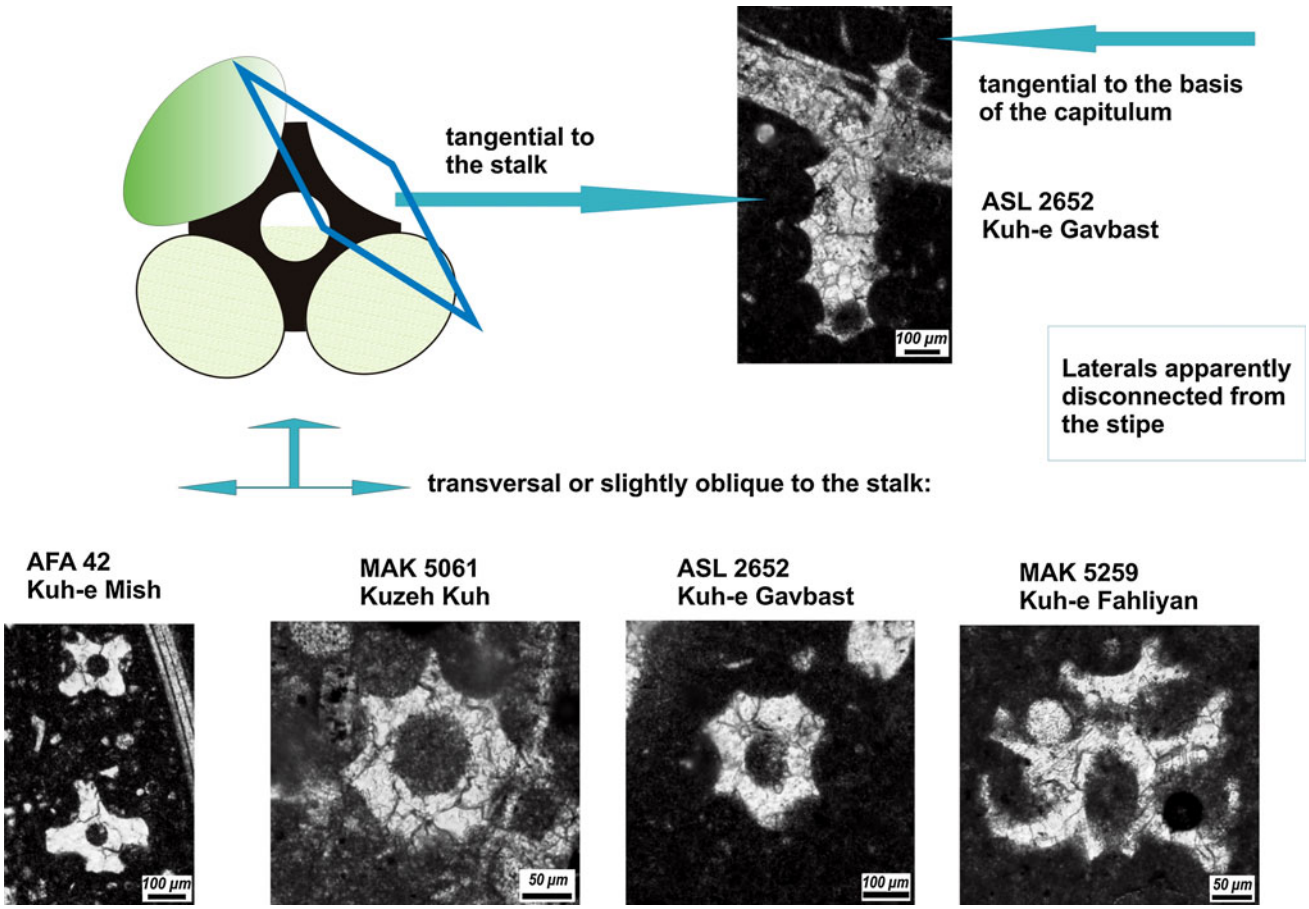

Fig. 12 Schematic reconstruction of the basal stalk of *Iranella inopinata*. Cysts missing or not visible

unusual combination of characters presumably reflects growth stages of the alga, and/or environmental bias. To our knowledge, it is reported for the first time in a dasycladalean alga and applies, at least to a certain extent and following the views of Barattolo et al. (2008), to the family Triploporellaceae. Quoting Berger and Kaever (1992, table 2.4) "This family is characterized by euspondyl arrangement of laterals and cladospore formation of gametangia." However, according to Barattolo et al. (2008), "Although the kind of reproduction (endosporous or cladosporous) is a high taxonomic character, their evidence is lacking in most of fossil taxa. The occurrence of thin and delicate laterals, irrespectively of whether trichophorous or phloiophorous, often associated with a bulky central stem, is considered a proof of an endosporous reproduction (for a discussion see De Castro 1997). Consequently, the diagnosis of Triploporellaceae ought to include both endosporous and cladosporous reproduction." At present, any other consideration on the systematic position of *I. inopinata* would be merely speculative.

The species closest to *I. inopinata* is the Oxfordian—Kimmeridgian *Conodictyum striatum*, known from reefal deposits in southern Germany. The genus *Conodictyum* is monospecific. Typical of *C. striatum* is a large (18-mm-long) club-shaped thallus, with costules (or nervures), laterals set on longitudinal files and laterals open at tips. *Conodictyum* was originally described as an animal. For details, reference is made to Bassoullet et al. (1978).

Distribution

The stratigraphic range (Fig. 2) is Berriasian-Aptian, as proven by foraminifers and other dasycladalean alga found by Hosseini and Conrad (2008), but was previously reported as a marker for the Barremian-Aptian in the Zagros area by Gollestaneh (1965, 1974, 1979). Its abundance is higher in the Valanginian.

Habitat and depositional environment

Vertical facies distribution and sequential interpretation reveals that *I. inopinata* becomes more common in the late transgressive and early highstand stages of system tracts. During these stages water depth is moderate, with a balanced situation between the accommodation and sediment

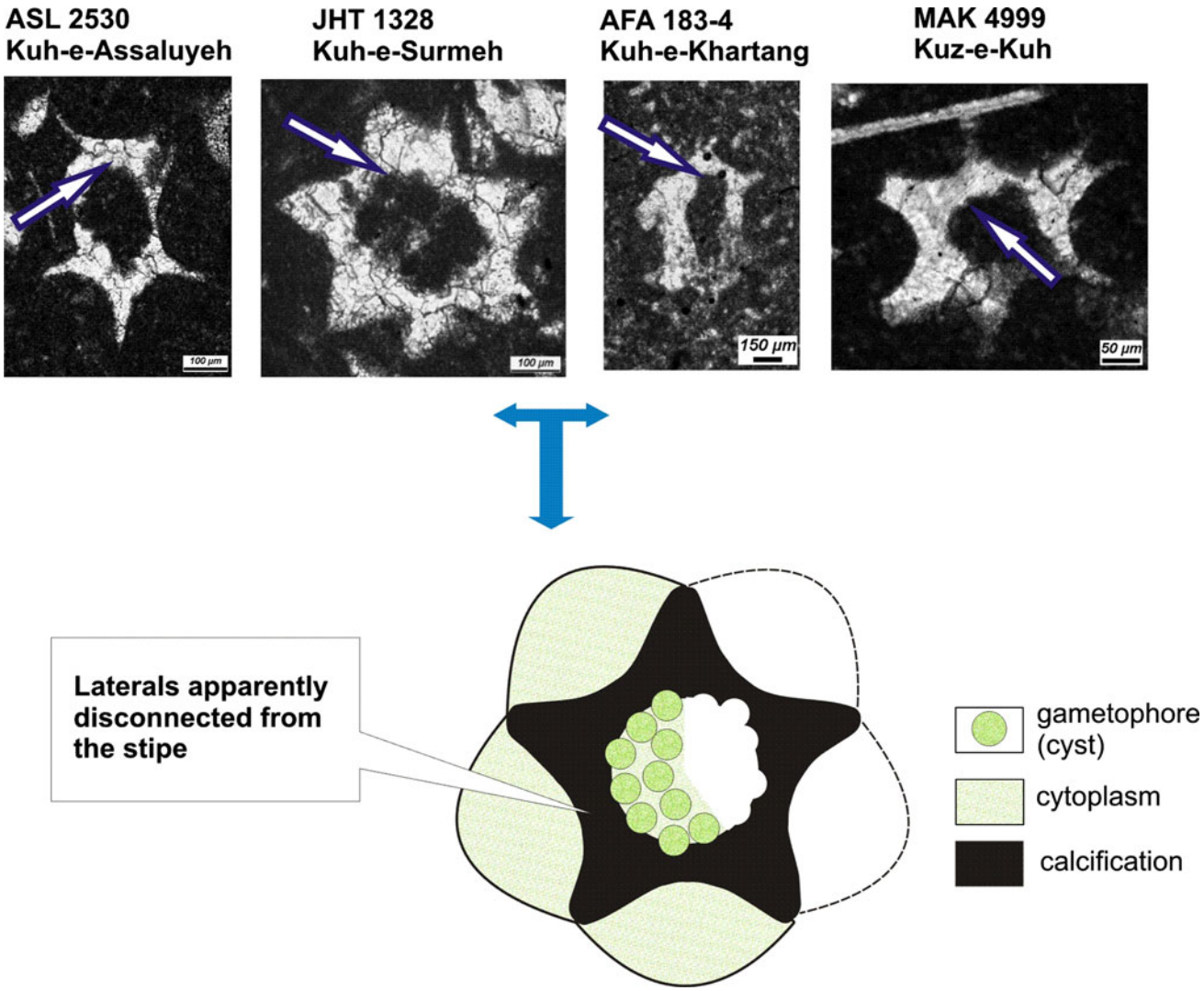

Fig. 13 Schematic reconstruction of the basal stalk of *Iranella inopinata*. Endospory (cysts present in the stipe) visible

supply. In order to recognize the habitat of *I. inopinata*, we identified the accompanying dasycladalean alga and interpreted these assemblages based on conclusions put forward by several authors, including Bucur and Sasaran (2005), Conrad (1977), Carras et al. (2006), Jaffrezo (1980), and Jaffrezo and Renard (1979). In the Berriasian-Hauterivian interval, *I. inopinata* is typically accompanied by *Salpingoporella annulata*, *S. piriniae*, *S.* aff. *piriniae*, *S. circassa*, *S. katzeri*, *S. istriana*, *Actinoporella podolica, A. jaffrezoi*, *Clypeina solkani*, *C. parasolkani*, *C. dragastani*, *C. estevezii*, *C. nigra*, *C. sudgeni*, *Otternstella lemmensis* and, occasionally, *Selliporella neocomiensis*. All of these species are (or at least are believed to be) cosmopolitan, that is they are found in the northern as well as southern Tethyan domains. They stand for platform-interior algal habitats, with restricted to semi-restricted seawater conditions and fluctuating salinities, deposition usually prevailing in subtidal lagoons or ponds.

Occasionally, *I. inopinata* co-occurs with *S. pygmaea*, a species characteristic of open-marine, reefal platform margin and medium-to-high energy conditions (Carras et al. 2006). It also occurs in deposits dominated by algal-rich wackestones and packstones, with high clay content, proving somewhat deeper depositional conditions. In the Barremian–Early Aptian Gadvan Formation, including the Khalij Member, and the Aptian Dariyan Formation, the last specimens of *I. inopinata* occur with *Salpingoporella dinarica*, a species endemic to the Southern Tethyan Domain. The size of *I. inopinata* looks as if environmentally controlled, with the Berriasian–Valanginian samples mostly large and heavily calcified, presumably because of favorable, platform-interior conditions, whereas most specimens from the Barremian and Aptian are dwarfed, and weakly calcified.

As suggested by the range chart distribution of *I. inopinata* (Fig. 2), during the Berriasian and Valanginian,

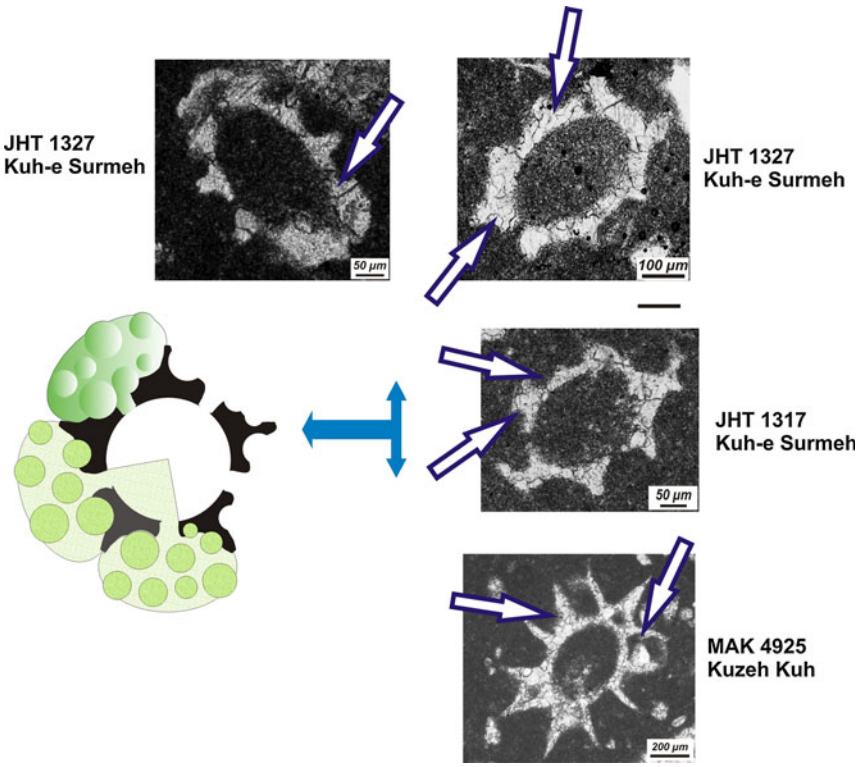

Fig. 14 Schematic reconstruction of the basal stalk of *Iranella inopinata*. Cladospory (cysts present in the laterals) visible

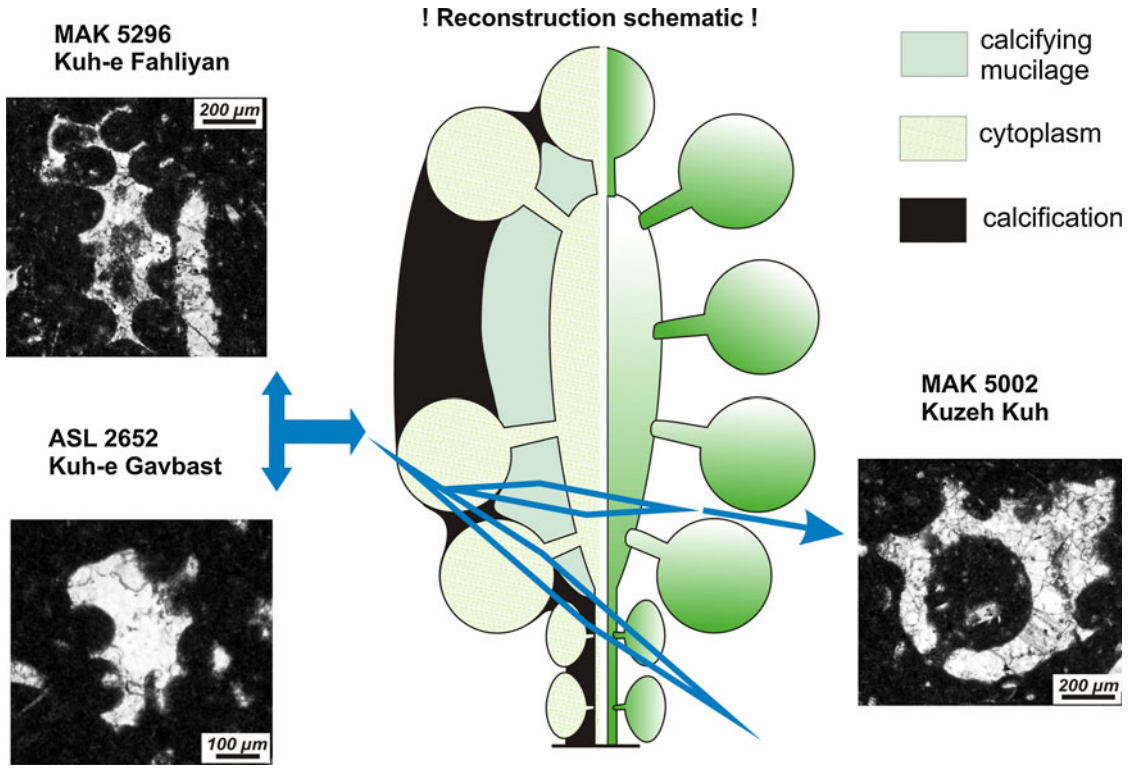

Fig. 15 Tentative, schematic reconstruction of the junction between the basal stalk and the capitulum of *Iranella inopinata*. The laterals of the capitulum are more or less free and compressed (MAK 5296)

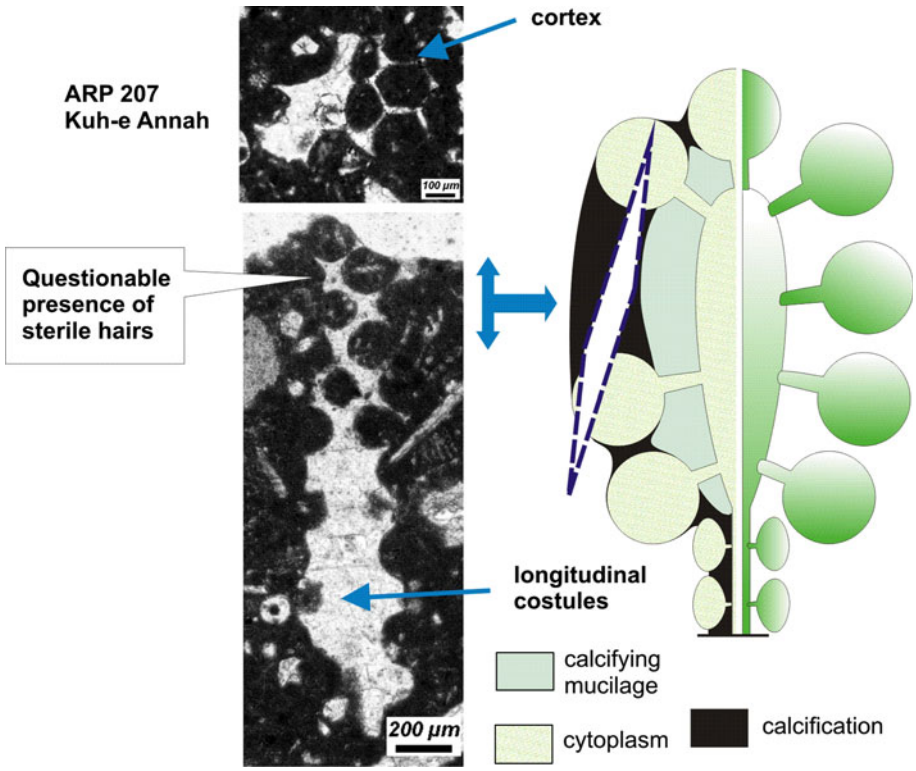

Fig. 16 Tentative, schematic reconstruction of the capitulum of *Iranella inopinata*, when higher-order laterals are missing. Distally, the laterals are clearly mutually compressed, polygonal (ARP 207)

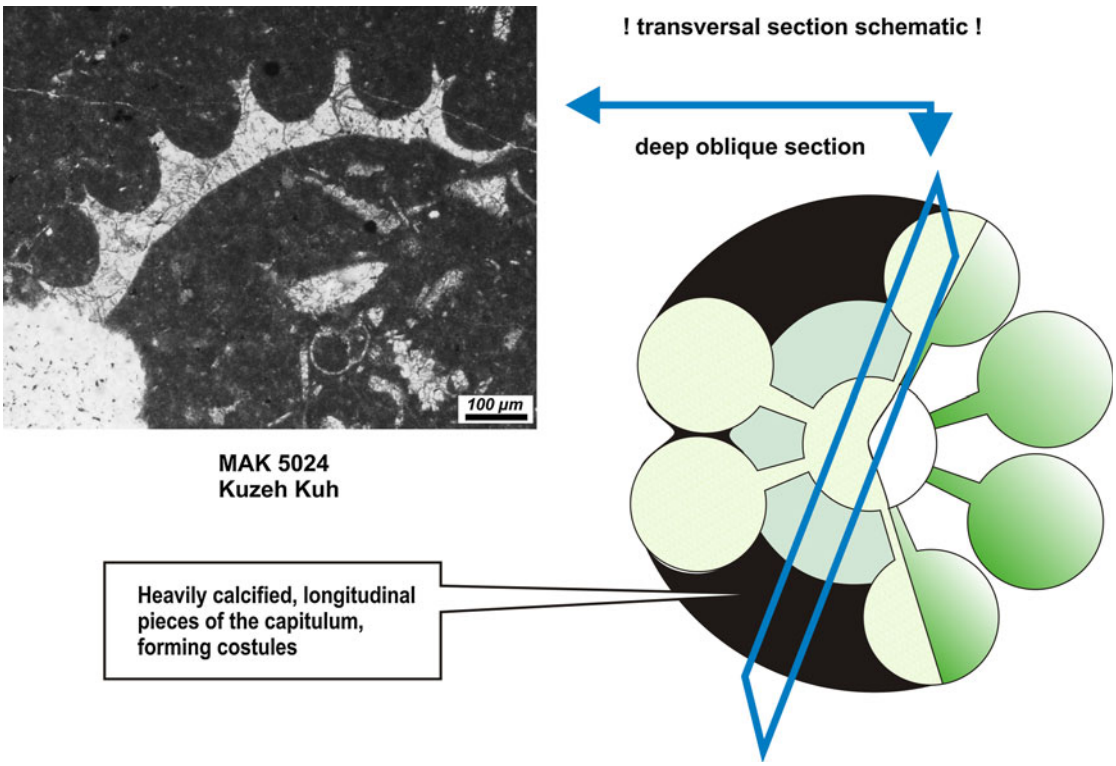

Fig. 17 Tentative, schematic reconstruction of a transverse section of the capitulum of *Iranella inopinata*

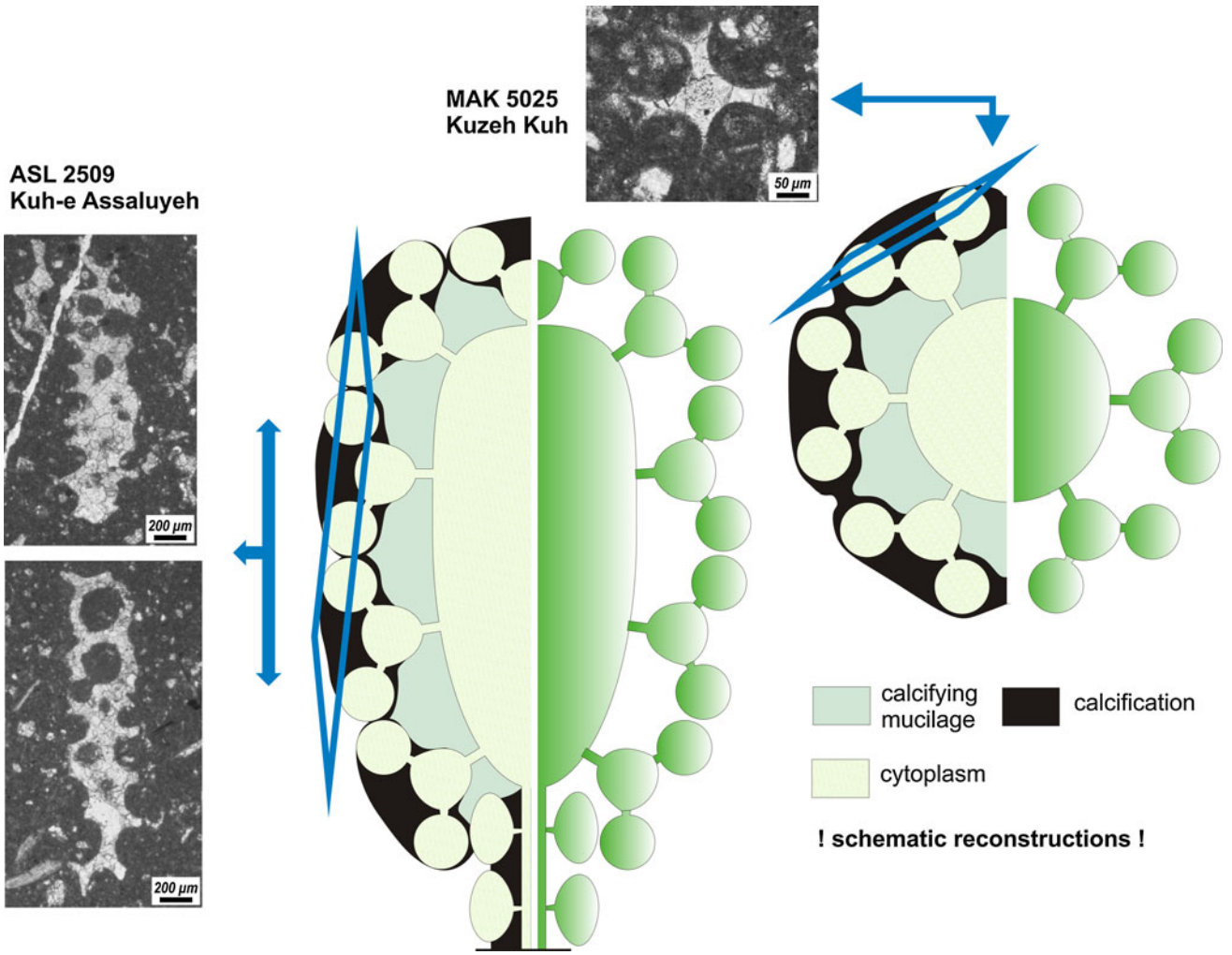

Fig. 18 Tentative, schematic reconstruction of an axial section of the capitulum of *Iranella inopinata*, with higher (?2nd) order laterals. Note that the two drawings are not at the same scale

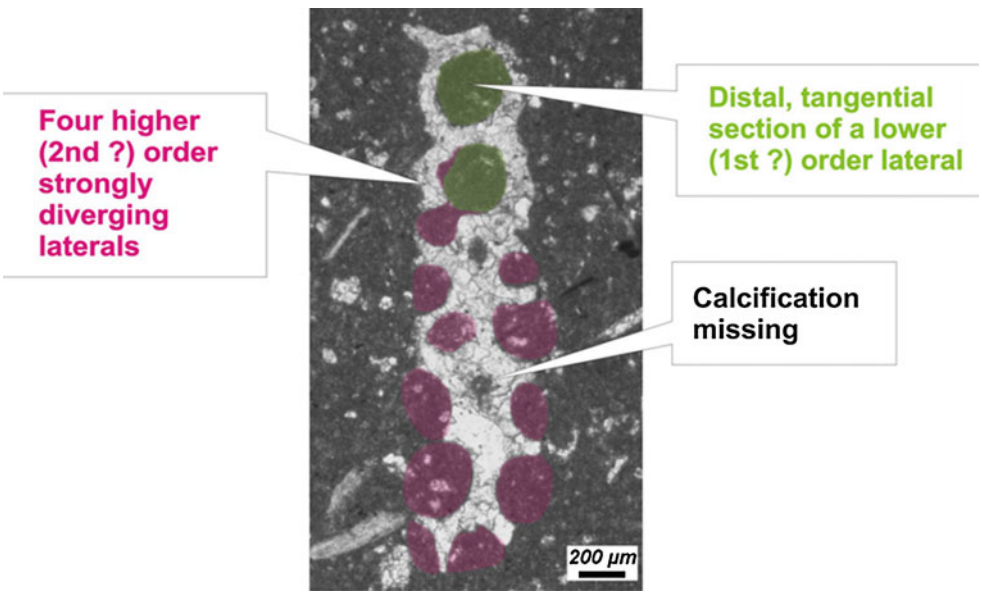

Fig. 19 Elongated piece of the capitulum, forming solid, strongly calcified, longitudinal costules. Evidence for higher-order laterals

a carbonate platform standing or restricted conditions favorable for the algal growth, was extending throughout the Zagros Basin. These conditions are true both of early transgressive and late highstand stages of system tracts. Thereafter conditions changed. During the Hauterivian, platform-interior conditions persisted westward in the Mangasht and Kuh-e Mish area, while platform-margin or top-platform conditions prevailed west and east, respectively, of the Kazerun fault in the Fahliyan area. During the Barremian, platform-margin or near-slope conditions prevailed in most parts of the study area, in which *I. inopinata* only sporadically occurs, accompanied by rare low-energy biota and *S. pygmaea*. The Bandar Abbas Hinterland (Kuh-e-Nakh, Kuh-e Khush, Kuh-e Genow) is an exception, however, still with rather restricted depositional environments, as shown by the presence of diversified and abundant algal assemblages including *I. inopinata*.

Biogeographic distribution

Iranella inopinata was first reported from the Zagros FTB. In this area, the species appears in the Berriasian, reaches its greatest abundance in the Valanginian, decreases during the Barremian, and becomes extinct in the Late Aptian (Fig. 2). Personal information dated 1995 and 2012 calls for the species to occur elsewhere on the Arabian Platform, in the United Arab Emirates and Oman, in the Early Cretaceous Kharaib and Shuaiba formations, and in Saudi Arabia. In the Berriasian-Hauterivian interval, *I. inopinata* is commonly accompanied by well-known, cosmopolitan species such as *Salpingoporella annulata*, *Actinoporella podolica,* and *Otternstella lemmensis*. In the Barremian and Aptian, it is associated with *Salpingoporella dinarica*, a species endemic to the southern Tethyan Domain. *I. inopinata* seems missing in other regions of the southern Tethyan and Eurasian (northern Tethyan) domains, for example in central Iran (Bucur et al. 2012) and the Kopet Dagh (Taherpour Khalil Abad et al. 2010). This is another case of species-specific endemism of certain dasycladalean alga. Hauterivian and Barremian deposits found in France, Switzerland and Spain, for example, contain, in addition to cosmopolitan species, numerous specimens of *Salpingoporella muehlbergii*, *S. genevensis,* and *Piriferella paucicalcarea*. *S. muehlbergii* occurs in the Kopet Dagh (Taherpour Khalil Abad et al. 2010) as well as in central Iran (Bucur et al. 2012). In contrast, none of the above-mentioned three species was identified in the Zagros Mountains. Endemism among the Dasycladalean algae is also known in the Recent, with species restricted to certain areas such as the Mediterranean, the Caribbean, and the Pacific Ocean.

Conclusions

Iranella inopinata is a dasycladalean alga endemic to the Arabian Platform. In the Zagros fold-thrust belt, the species is found in the Fahliyan, Gadvan, and Dariyan limestone formations, ranging from the Berriasian to the Aptian, with an acme period in the Valanginian. Deposition took place in low-energy, protected or semi-protected environments in the late transgressive and early highstand stages of system tracts. The species was originally, although invalidly, described by Gollestaneh (1965) as an incertae sedis. It was later provisionally assigned by Hosseini and Conrad (2008) to the dasycladalean algae. New material, collected from a number of outcrops, leads to an extensive, although yet not entirely satisfactory revision of the taxonomy of this form. Based on diversely oriented algal fragments, reconstructions prove the thallus to be twofold, with a conspicuous, strongly calcified basal stalk, and an upper, incompletely calcified but costulated capitulum. Up to a certain extent, *I. inopinata* is comparable to *Conodictyum striatum*, a species known from the Late Jurassic of southern Germany. In several specimens, imprints of cysts (reproductive organs) are present in the stalk of *I. inopinata*, either within the stipe (endospory), or the laterals (cladospory), proving a unique combination of phylogenetically highly significant characters. Consequently, the genus *Iranella*, originally introduced by Gollestaneh (1965), is validated, as a new, so-far-monospecific, genus of dasycladalean algae.

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